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Linnæus defined a plant as an organized, living, but non-sentient body and an animal as an organized, living, and sentient body. Although no modern biologist would attempt to support the contention that animals are sentient and plants are not, the distinction drawn by Linnæus is not without a certain foundation in truth, for sentience in its full development and as Linnæus probably understood it, is the exclusive and supreme possession of the higher animals. That these animals possess intelligence as contrasted with all other natural bodies is a statement to which few naturalists will offer any serious objection. The seat of this intelligence is the nervous system and, though the integrity of the other systems of organs is essential in most cases to the well-being of the animal body, the fact that the totality of activities that makes up the mental life of human beings as well as that of other animals, is absolutely dependent upon the nervous system, is evidence sufficient of the paramount importance of these organs. It is, therefore, not without interest to inquire into the origin of this system of organs and to trace the early steps by which it passed from a position of initial obscurity to one of the highest significance.

The nervous system of the higher animals, though enormously complex in its organization, is composed of relatively simple elements, the neurones, arranged upon a comparatively uniform plan. This plan is well exemplified in the spinal cord of the vertebrates. In this organ the sensory neurones, whose cell-bodies lie in the dorsal ganglia, extend from the integument through the dorsal roots to the gray matter of the cord. Motor neurones, whose cell-bodies are situated within the gray matter of the cord, reach from this region to the muscle-fibers which they control. These two classes

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of neurones would seem to be sufficient for all ordinary reflex operations, but the cord contains within its limits many other neurones which serve to connect one part of its structure with another. These neurones, therefore, have been called association neurones, a term which has unfortunately proved to be somewhat misleading because of its use in psychology for quite a different range of phenomena. The so-called association neurones are interpolated between the sensory and motor elements just described and must thereby lengthen and extend the courses of the reflex impulses. Such neurones make up a large part of the substance of the cord and doubtless increase enormously its internal connections. In the brain they not only add to the nervous interrelations, but they afford in the region of the cerebral cortex the material basis for all intellectual operations.

The plan of neuronic arrangement as exemplified in the vertebrates also obtains in animals as lowly organized as the earthworm. In this form the sensory neurones, whose cell-bodies are situated in the integument instead of being gathered into special ganglia, extend, as in the vertebrates, from the skin to the central nervous organs, the brain or the ventral ganglionic chain. The motor neurones are essentially duplicates of those in the vertebrates in that their cell-bodies lie within the central organs whence their fibers extend to the appropriate musculature. Association neurones are also abundantly present in the earthworm though their function here, in contrast with that in the higher vertebrates, is pure nervous intercommunication, for it is very unlikely that the earthworm possesses what in any strict sense of the word can be called intelligence. Thus from a morphological standpoint, the nervous systems of the higher animals, even including such forms as the earthworm, have much in common, their three sets of interrelated neurones, sensory, motor, and association, being arranged upon an essentially uniform plan.

Considered from a physiological standpoint, the nervous system with its appended parts as just sketched falls in the higher animals into three well marked categories. On the exterior of these animals, are to be found sense organs or receptors such as the free-nerve terminations of the sensory neurones in the vertebrates or the sensory cells in the integument of the earthworm. These organs have for their function the reception of the external stimuli and the production of the sensory impulses. The receptors are connected by nerve-fibers with the central nervous organ or adjustor composed of the central ends of the sensory and the motor neurones and of the association neurones. Here the impulses arriving from the receptors are directed toward the appropriate groups of muscles by which the animal may respond to the stimulus and, if the animal is highly organized, impressions are made upon the adjustor which, as memories, may become more or less permanent parts of the animal's nervous equipment. Finally the adjustors are connected by nerve-fibers with the third set of elements, the effectors, which as muscles, electric organs, glands, etc., enable the animal to react on the environment. Thus three physiological categories are to be distinguished which in the order of their sequence in action are sense organs or receptors, central nervous organs or adjustors, and muscle, etc., or effectors.

It is to be noted in passing, that the physiological scheme just outlined includes a wider range of parts than is generally admitted under the head of the nervous system. The additional parts are the effectors, which, as will be shown later, form as truly a part of the whole system as do the sense organs or the central nervous organs. Since the term nervous system does not ordinarily include the effectors, it is perhaps best to designate the whole chain of related parts, receptors, adjustors, and effectors, as the neuromuscular mechanism and in dealing with the origin of the nervous system, it will be found important to keep this relation in mind, for in such an inquiry, the real question that must be confronted is the origin of the neuromuscular mechanism rather than that of the nervous system alone.

The type of neuromuscular mechanism described in the preceding paragraphs in which a group of receptors is connected with a well centralised adjustor which in turn controls a complex system of effectors, is found only in the more differentiated metazoans. Certainly in the simple metazoans, like the jellyfishes, corals, sea-anemones, etc., only the slightest evidence of this type of nervous organization can be discovered. Nevertheless these animals possess a neuromuscular mechanism but on so simple a plan that investigators have long been inclined to regard it as representing the first step in the differentiation of the neuromuscular organs. This plan of structure is well represented in the sea-anemones. Each of the two chief layers of cells that make up the living substance of the sea-anemone's body consists of three sublayers: a superficial or epithelial layer, a middle or nervous layer, and a deep or muscular layer. The epithelial layer contains, besides many other kinds of cells, large numbers of sensory cells which terminate peripherally in bristle-like receptive ends and centrally in fine nervous branches. These fine branches constitute collectively the middle or nervous layer in which occasionally large branching cells, the so-called ganglionic cells, occur. Immediately under the nervous layer is the deep layer of elongated muscle-cells. The condition thus briefly described is present over the whole of the sea-anemone's body and though the nervous layer is somewhat emphasized in the neighborhood of the mouth, it cannot be said to be really centralised in any part. Hence this type of nervous system has been designated as diffuse in contrast with the centralised type found in the higher metazoans.

Not only is the structure of the nervous system of the sea-anemone appropriately described as diffuse, but in its action this system shows those peculiarities that would be expected from the possession of so diffuse an organization. Since each part of the animal contains its own nerve and muscle, it is not surprising that after isolation many of these parts will respond to stimuli much as they did when they were a constituent of the whole organism. Tentacles, for instance, when freshly cut from the body of a sea-anemone will respond to pieces of food by encircling them, etc., in much the same way as when these organs were parts of a normal animal. Much evidence of this kind has shown conclusively that the nervous system of cœlenterates is no more centralized physiologically than it is anatomically, but is in all respects essentially diffuse.

What is really present in the neuromuscular portion of the sea-anemone's body is a large number of peripheral sensory cells whose deep branching ends connect more or less directly with the muscles, *i. e.*, without the intervention of a true central organ. This neuromuscular system, if described in the terms already used, could be said to be composed of receptors and effectors without an adjustor or at least with this member present in only a most primitive state. In my opinion this is the condition in most cœlenterates. Judging from the more recent work on the nervous organs of these animals, centralization can scarcely be said to be present at all in hydra; it is but little more pronounced in the sea-anemone; and, though most marked in the jellyfishes, it does not rise even here to a grade that entitles it to comparison with what is seen in such forms as the earthworm. The cœlenterates, then, are animals possessing receptors and effectors but without developed adjustors. Hence the adjustor or central organ is in all probability an acquisition that represents a later stage in the development of the neuromuscular mechanism than that seen in the cœlenterate.

If the cœlenterates represent a stage in the evolution of the neuromuscular mechanism in which sensory cells and muscles are the only important parts present, it is natural to ask if there is not a still more primitive state from which the cœlenterate condition has arisen. On this question several hypotheses have already been advanced. Claus and, subsequently, Chun maintained that originally the nervous system and the muscles were differentiated independently and that they became associated only secondarily. This view has deservedly received very little attention, for not only is it difficult to conceive that an animal would develop receptive ability without at the same time acquiring the power to react, but not a single example among the lower animals is known in which developed nerve and muscle are present and independent of each other.

Much more worthy of consideration than the hypothesis of the independent origin of nerve and muscle is Kleinenberg's theory of the neuromuscular cell. In 1872 Kleinenberg announced the discovery in the fresh-water hydra of what he designated as neuromuscular cells. The peripheral ends of these cells were situated on the exposed surface of the epithelium, of which they were a part and were believed to act as nervous receptors; the deep ends were drawn out into muscular processes and served as effectors to which transmission was supposed to be accomplished through the bodies of the cells. Each such cell was regarded as a complete and independent neuromuscular mechanism, and the movements of an animal provided with these cells was believed to depend upon the simultaneous stimulation of many such elements. It was Kleinenberg's opinion that these neuromuscular cells (Fig. 1, *B*) divided (*C*) and thus gave rise to the nerve-cells and muscle-cells (*D*) of the higher animals. In fact he declared that the nervous and muscular systems of these animals were thus to be traced back to the single type of cell, the neuromuscular cell, which morphologically and physiologically represented the beginnings of both. But Kleinenberg's neuromuscular cells were subsequently shown by the Hertwigs to be merely epitheliomuscular cells and no intermediate stage between them and the differentiated neuromuscular mechanism of higher forms was ever discovered. Hence this hypothesis, too, has been largely abandoned.

FIG. 1. Diagram to illustrate Kleinenberg's theory of the neuromuscular cell. *A*, epithelial stage; *B*, neuromuscular cell; *C*, neuromuscular cell partially divided; *D*, nerve-cell and muscle-cell of cœlenterate stage.

Some years later, in 1878, the Hertwigs published an account of the neuromuscular mechanism in cœlenterates, an account which even at the present time is accepted as authoritative by most students of the subject. In this account they described the sensory cells, the ganglionic cells, and the muscular cells of the cœlenterates, and maintained that these elements arose not by the division of single cells, as implied in Kleinenberg's hypothesis, but that each element was differentiated from a separate epithelial cell (Fig. 2) and yet in such a way that during differentiation all these elements were physiologically interdependent. This hypothesis of the simultaneous differentiation of nerve and muscle is the current opinion among biologists today.

As opposed to Hertwigs' hypothesis of the origin of nerve and muscle, I wish to present certain facts obtained from a study of sponges. As is well known, sponges are extremely primitive metazoans, more primitive even than the cœlenterates. All attempts to demonstrate in them sensory or other nervous structures have yielded negative results, so that the majority of investigators of this group have come to regard sponges as devoid of true nervous structures. Not only are sponges without parts that can be reasonably called nervous, but so far as I have been able to ascertain by an extended study of a species of *Stylotella,* they show none of those qualities of transmission and relatively quick reaction which characterize even such animals as have only primitive nervous systems. In fact in this respect sponges resemble plants rather than animals. But notwithstanding the fact that sponges show no evidence either anatomical or physiological of possessing nervous organs, they are not without powers of response. *Stylotella,* for instance, can open and close its oscula and its lateral pores, and can even contract its flesh more or less. These movements, to be sure, are carried out very slowly, but they follow certain stimuli with such regularity that they must be regarded as true responses. Thus the oscula of this sponge close regularly when the water about these openings becomes quiet and reopen after the water has been again set in motion. These movements of the sponge are carried out by contractile tissue which has the appearance of smooth muscle-fiber and which, like smooth muscle, responds with great slowness. The slowness of the response is so marked even in comparison with what is met with among the

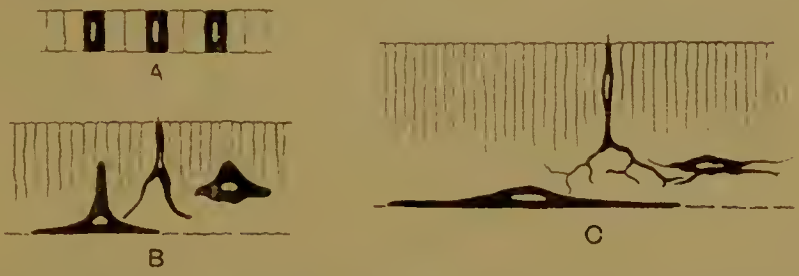

FIG. 2. Diagram to illustrate Hertwigs' theory of the origin of nerve and muscle. *A,* epithelial stage; *B,* partially differentiated muscle-, nerve- and ganglion-cell; *C,* muscle-, nerve- and ganglion-cell of cœlenterate stage.

more sluggish cœlenterates, as to suggest that the muscles in question act not through the intervention of nerves, but under direct stimulation, and since sponges have yielded no evidence anatomical or physiological of possessing nervous elements of any kind, I have concluded that their muscles normally act under direct stimulation. In other words, sponges are metazoans with effectors but without receptors; and in so far as their neuromuscular mechanism is concerned, they are metazoans one degree simpler than the majority of cœlenterates.

If this conclusion concerning the neuromuscular mechanism in sponges is correct, it follows that, of the three elements concerned, the effector or muscle is the most primitive and has developed as an organ quite independent of nerve, as seen in the sponges (Fig. 3, *A*, *B*). Next in sequence would appear the receptor or sense organ which, derived from the cells in the neighborhood of a developed effector (*C*), would serve as a more efficient means (*D*) of calling this organ into action than direct stimulation. This stage is represented by many cœlenterates; and their quick responses, as compared with those of sponges, are dependent, I believe, upon this advance in organization. Finally, in forms somewhat more advanced than the cœlenterates, central nervous organs or adjustors would begin to differentiate in the region between the receptors and effectors; and these would develop in the higher animals, first, as organs of transmission whereby the whole musculature of a given form could

FIG. 3. Diagram to illustrate the early stages in the differentiation of the neuromuscular mechanism. *A*, epithelial stage; *B*, differentiated muscle-cell at stage of sponge; *C*, partially differentiated nerve-cell in proximity to fully differentiated muscle-cell; *D*, nerve- and muscle-cell of cœlenterate stage.

be brought into coördinated action from a single point on its surface and, secondly, as the storehouse for the nervous experience of the individual and the seat of those remarkable activities that we recognize in the conscious states of the higher animals. Thus nerve and muscle did not develop independently, as claimed by Claus and Chun, or simultaneously, as maintained by Kleinenberg and the Hertwigs, but muscle appeared first as independent effectors and nerve developed secondarily in conjunction with such muscles, first as a means of quickly setting them in action and, secondly, as a seat of intelligence.

When we survey the whole range of metazoan development, we cannot but be struck with the remarkable history of the neuromuscular mechanism. The earliest metazoans were doubtless little more than colonies of protozoan cells concerned with the common functions of feeding and reproduction and conforming more or less to Haeckel's hypothetical gastræa. To these early functions of this primitive metazoan were added colonial reactions in that a system of independent effectors, more or less such as we see in the musculature of the modern sponge, was differentiated. As a means of bringing this musculature into more effective response, nervous elements developed in close proximity to the effectors. With the growth of the musculature and the nervous system in volume and with the consequent increase of metabolism, came the development of the circulatory system and its dependencies, the respiratory and the excretory organs. Thus the relatively simple body of the primitive metazoan became gradually converted into that of the more complex type. In all these changes no system of organs has done so much to unify the metozoan body as the nervous system. If a sponge may be outlined as a metazoan whose organization concentrates on feeding and reproduction, a human being may be described as one whose organization centers around nervous action. In such an organism the nervous system is supreme; and the rest of the body may be said to do little more than afford a favorable environment for this system; and yet, if the preceding account is correct, this most important system originated somewhat late in the history of the metazoa and as a relatively insignificant organ for the discharge of muscular activity.

Harvard University,
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